FUNCTION OF CHEMORECEPTOR ORGANS IN SPATIAL ORIENTATION OF THE LOBSTER, *HOMARUS AMERICANUS*: DIFFERENCES AND OVERLAP

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ABSTRACT

Three of the lobster's main chemoreceptor organs, the lateral and medial antennules (representing smell) and the dactylus-propodus segments of the walking legs (representing taste), are physiologically quite similar. We examined their role in spatial orientation in a food-odor stimulus field.

Control animals almost always oriented correctly and immediately to an odor plume. Lobsters with unilateral ablations of lateral antennules lost this ability, but did not show preferential turning toward the intact side. Unilateral medial antennule ablation did not affect orientation. Removal of all aesthetasc hairs from one lateral antennule caused loss of orientation ability less severe than unilateral ablation of the entire lateral antennule. Lobsters with unilaterally ablated lateral antennules and blocked walking leg receptors turned preferentially toward the side of the intact antennule.

Thus, it appears that intact lobsters orient in odor space by tropotaxis principally using aesthetasc receptor input. The first two pairs of walking legs and non-aesthetasc receptors on the lateral antennule have additional roles in spatial chemical orientation. The medial flagellum does not contribute to orientation. Since loss of appendages is relatively common in lobsters, this partial overlap of organ function may serve the animal well in nature.

INTRODUCTION

In the American lobster, searching for food may be elicited and maintained by chemical cues alone. In order to search efficiently the lobster must be able to identify a chemical cue and extract directional information from a chemical stimulus field. Several bilateral chemoreceptor organs located on different appendages must be considered as possible mediators of distance orientation.

The biramous antennules are usually considered the distance chemoreceptors in decapod crustaceans (Maynard and Dingle, 1963; Hazlett, 1971). In particular, the aesthetasc hairs of their lateral flagellum are implicated as being chemoreceptors by morphological (Laverack, 1964; Laverack and Ardill, 1965; Ghiradella *et al.*, 1968), electrophysiological (Ache, 1972; Shepheard, 1974), and behavioral studies (McLeese, 1970, 1973, 1974; Snow, 1973; Reeder and Ache, 1980). Walking leg and maxilliped chemoreceptors have been described respectively as "outer" and "inner" contact chemoreceptors (Luther, 1930). On the walking legs the regions of greatest receptor density and specialization are the dactylus and propodus (Derby and Atema, 1982a); the walking leg chemoreceptors are often incorrectly called

dactyl receptors. Specific chemoreceptor sensilla on dactylus and propodus have been identified in crayfish (Hatt and Bauer, 1980), and in the lobsters *H. gammarus* (Shelton and Laverack, 1968, 1970) and *H. americanus* (Derby, 1982). Roles of these different chemoreceptor organs in feeding behavior of *H. americanus* were described by Derby and Atema (1982b). The external appearance of chemoreceptor sensilla may have been shaped by their micro-environments; for example, antennular chemoreceptors remain in the water column, while leg chemoreceptors are subjected to abrasion when the lobster is walking or probing in the substrate (Atema, 1980). Despite morphological differences of sensilla, primary receptor cells of antennules and walking legs may be quite similar in response spectrum and threshold. Although earlier studies found leg chemoreceptors to have higher thresholds than antennular receptors (Case and Gwilliam, 1961; Ache, 1972; Shepheard, 1974; Fuzessery and Childress, 1975; Fuzessery *et al.*, 1978), recent work has shown that both leg (Derby and Atema, 1982a) and antennular receptors (Thompson and Ache, 1980) can have thresholds lower than previously known. Based on their physiology both antennules and legs could be efficient distance chemoreceptors. Studies which correlate this physiological and morphological information with behavioral function are scarce, and the labels "contact" and "distance" chemoreceptor are based on casual observation only. However, based on neuroanatomical and behavioral criteria, the crustacean antennules can be called smell organs and the legs and maxillipeds taste organs in analogy with vertebrates and in homology with insects (Atema, 1980).

An increase in the rate of antennule flicking, *i.e.,* the periodic depression of the lateral flagellum of the antennule, is generally one of the first observable changes in behavior after chemical stimulation. This behavior has been used to determine chemical detection thresholds (Pearson and Olla, 1977). Thresholds are effectively lowered by flicking (Schmitt and Ache, 1979). Flicking—functionally similar to sniffing by terrestrial vertebrates—may well compensate for the haphazard spatial and temporal character of a chemical stimulus field. This and both physiological (Fuzessery, 1978) and behavioral evidence (McLeese, 1973; Reeder and Ache, 1980) strongly argue for the importance of the lateral flagellum in spatial orientation. After bilateral ablation of the aesthetasc-bearing flagella, spiny lobsters did not search in response to food odor, whereas ablation of the medial flagella did not interfere with searching behavior (Reeder and Ache, 1980). This animal uses both tropotactic and klinotactic components in orientation to food odors.

This study shows that *H. americanus* appears to orient to odors principally by means of the aesthetasc receptor input, that other chemoreceptors on the lateral flagellum of the antennules may contribute somewhat to orientation, and that the walking leg chemoreceptors function in orientation when aesthetasc input is impaired.

MATERIALS AND METHODS

Materials and apparatus

Lobsters used in this study (carapace length 60–82 mm) were captured by local fishermen in the waters off Woods Hole, Massachusetts. They were maintained in holding pens in running seawater for at least two weeks prior to placement in testing tanks.

All tests were done in three identical 675-liter fiberglass aquaria measuring 1.25 m long × 0.9 m wide × 0.6 m deep with glass fronts. Each tank was outfitted with a biologically conditioned sub-gravel filter and filled with either natural or

artificial seawater. Illumination was provided by a 40 W bulb suspended 1 m above the water surface. The light cycle approximated natural sunrise and sunset for that particular time of year. The water temperature varied from 18 to 22°C. A single animal was kept in one tank for the entire length of an experiment. Animals were allowed a minimum acclimation period of two days before any tests were run. The lobsters were fed daily on a diet of cod muscle (*Gadus callarias*), but never to satiation; they were never fed at the odor source locations used in tests.

Each tank was fitted with a double symmetrical recirculating seawater system as described by Atema and Gagosian (1973). The airlift water intakes were above the lobster's shelter, in the rear center of the tank. Each intake delivered an irregular flow of about 25 ml/sec. Funnel interruptions in both sides of this system allowed introduction of a chemical stimulus without appreciable (2–3%) concurrent novel mechanical stimulus. A 2–4 min time delay further separated chemical stimulus arrival from possible contamination with a mechanical stimulus. Water flowed down the stem of the funnel to a right angle glass elbow facing perpendicular to the side of the tank and located approximately 4 cm from the bottom of the tank. This outflow was covered with rocks and located inside the center hole of a three-hole cinderblock to protect the all-glass system from the test animals (Fig. 1).

The stimulus used was an extract of homogenized and filtered cod muscle at a concentration of 5 g wet weight/l water. The stimulus side was semi-randomly switched between left and right; however the total number of trials was divided equally between the two sides. The stimulus was presented by pouring a 2-ml dose into the funnel over a 3-sec interval. Dye studies showed that traces of the stimulus remained in the funnel system for up to 30 sec, and that the dye pulse was visible at the shelter between 2 and 4 minutes after introduction. This variation in arrival times was due to variation in water currents between tanks; variation among tests within each tank was 15–30 sec (N = 4). The stimulus pulse had been diluted by a factor of 10^3 to 10^4 upon reaching the lobster in its shelter as measured by colorimetric analysis with methylene blue dye. The stimulus front moving from these outflows approached perpendicular to the length of the lobster in the shelter; the odor space appeared typically haphazard with whirls, lines, and pockets of various concentrations of dye.

Testing methods

Observations were made in a darkened room with the observer seated in front of the tank. All observations were made during the day. Lobsters are naturally nocturnal. Light keeps them in shelter, but when low enough it does not prevent them from searching when a chemical food stimulus is presented. All trials were run as described below.

Once the lobster was quiet and in its shelter, a single stimulus dose was introduced into the tank via the funnel system. The following three measurements on orientation were made: latency to alert, initial direction choice, and search path. The time period from stimulus introduction to the lobster's first behavioral response, "alert," was recorded. Among various possibilities we chose to define "alert" as distinct waving and pointing of the second (large) antennae and sudden body movements. If no alert response was observed within 8 minutes, an animal was recorded as giving "no response." Following alert and upon exit from the shelter, a searching lobster made an initial direction choice, either to the left or right of an imaginary line down the center of the tank. References to handedness always refer to the perspective of a lobster in its shelter, not to the observer. This initial direction
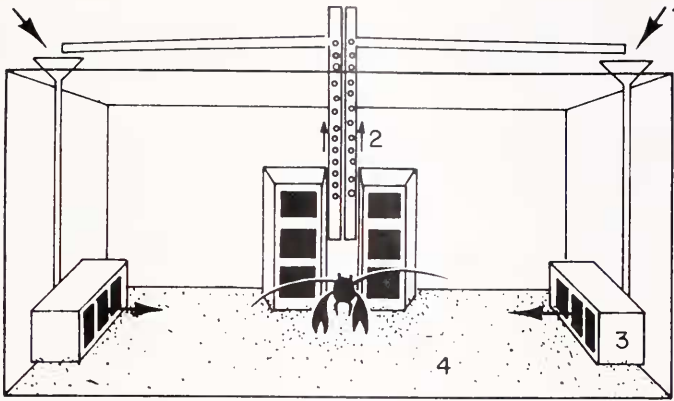
FIGURE 1. Diagram of test aquarium: (1) chemical stimulus, (2) air lift, (3) brick, (4) gravel substrate.

choice was scored as either "+" or "−" with respect to the stimulus side or "no response" if searching was not elicited. A sketch was made of the path taken by the test animal while it searched for the stimulus source. A test was considered completed when either an animal located the stimulus source or 10 minutes had elapsed since the introduction of the stimulus. The search path lengths were subsequently measured with a planimeter and converted back to actual distances walked by the test animal. Although preliminary tests showed that a lobster's performance was not affected by tests as close together as 1.5 hours, 3 to 12 hours were generally allowed between tests. Two to four tests were run per animal per day.

Treatment groups

The experiments were organized into four treatment groups of six lobsters each. In all groups, fifteen trials were run per animal to establish a baseline. The same number of trials was run on each animal after each phase of treatment. The treatments were: 1) The right lateral antennular flagellum was ablated, then the right medial flagellum was subsequently ablated. 2) The sequence of treatment 1 was reversed: ablation of the right medial flagellum was followed by right lateral antennular ablation. 3) The aesthetasc hairs of the right lateral flagellum were shaved off with a scalpel while the lobster was cold-anaesthetized on its back in a tray of ice. Once the experiment was completed, the shaved flagella were removed and prepared for scanning electron microscopy. 4) The dactylopodite and propodite of all four pairs of walking legs as well as the seizer claw were coated with the cyanoacrylate adhesive KrazyGlue® which formed a waterproof acrylic "glove" around the leg when dry. The use of cyanoacrylates does not result in non-specific behavioral changes in *H. americanus* (Derby and Atema, 1982b; C. Derby, unpublished data). These animals underwent subsequent ablation of the right lateral antennular flagellum. The right side of all animals was consistently used for ablation since there is no evidence for dominance of left or right in processing chemosensory input. Eighteen-hour recovery periods were allowed following all treatments for recovery from the effects of ablation and handling.

Friedman's analysis of variance by ranks (X_r^2) and multiple comparisons for ranked data were performed using the sums of each fifteen-trial group (Zar, 1974).

For presentation purposes, means and standard errors were calculated for each treatment group. Significance was accepted at the 0.05 level.

RESULTS

Normal lobsters initially responded to cod muscle extract by waving their antennae, increasing the rate of antennule flicking, and changing body stance and claw posture from resting to walking. Following this alert response and a short wait in the shelter, the lobster left the shelter in search of the odor source. Initial direction choice was almost always correct (347 times out of 360 tests). Searching consisted of walking a generally straight path to the odor source while doing much antenna waving, antennule flicking, fanning the exopodites of the maxillipeds, pleopod beating, and occasional wiping of antennules by the third maxillipeds. Within one body length of the odor source, the animals often probed the substrate with walking legs and maxillipeds. Upon reaching the odor source, normal animals would attempt to reach the outflow by inserting their first and second walking legs into the cinderblock where the odor outflow was hidden. They often persisted in this directed search behavior for several minutes.

None of the treatments affected either the lobster's use of antennae and walking legs in searching or their probing with walking legs and moving of maxillipeds. Also, none of the treatments affected alert latency (Tables I and II). However, in

TABLE I

Effects of chemoreceptor appendage ablations on three behavioral parameters.

	Alert latency (sec) $\bar{X} \pm$ SEM	Correct direction choice (15 trials)	Search path length (cm)
Group 1			
a) Untreated	106.7 ± 9.5	14.3 ± 0.3	159.3 ± 30.0
b) Right lateral ablation	102.2 ± 9.8	7.8 ± 0.3	250.5 ± 34.3
c) Subsequent right			
medial ablation	91.5 ± 14.9	8.0 ± 0.4	218.5 ± 33.5
Statistic and significance	$X_r^2 = 5.33$ NS	$X_r^2 = 9.08$ $P < 0.02$	$X_r^2 = 10.3$ $P < 0.01$
Group 2			
a) Untreated	153.0 ± 16.0	14.2 ± 0.3	105.3 ± 4.7
b) Right medial ablation	164.2 ± 17.9	14.8 ± 0.2	103.5 ± 3.7
c) Subsequent right			
lateral ablation	171.2 ± 21.2	8.8 ± 0.5	209.2 ± 14.8
Statistic and significance	$X_r^2 = 2.3$ NS	$X_r^2 = 9.34$ $P < 0.01$	$X_r^2 = 9.33$ $P < 0.01$
Group 3			
a) Untreated	171.2 ± 14.4	14.7 ± 0.2	111.7 ± 10.0
b) Right aesthetascs			
shaved	195.7 ± 20.0	9.8 ± 0.8	236.8 ± 35.5
Statistic and significance	$X_r^2 = 2.6$ NS	$X_r^2 = 6$ $P < 0.05$	$X_r^2 = 6$ $P < 0.05$
Group 4			
a) Untreated	167.3 ± 20.7	14.7 ± 0.2	98.0 ± 3.3
b) Glue-covered legs	172.8 ± 24.0	14.8 ± 0.2	110.2 ± 4.9
c) Subsequent right			
lateral ablation	180.8 ± 22.2	8.3 ± 1.0	271.3 ± 12.9
Statistic and significance	$X_r^2 = 5.33$ NS	$X_r^2 = 9.0$ $P < 0.02$	$X_r^2 = 9.33$ $P < 0.01$

NS = not significant.

TABLE II

Behavioral changes in food odor orientation after chemoreceptor appendage ablations.

Group	Ablations	Change in alert latency	Correct direction choice (%)		Change in search path length (%)		Circus movement
1a	None	—	94		—		no
1b	Lateral (L)	no	52°		+71**		no
1c	L + M	no	53°		+44**		no
2b	Medial (M)	no	99	*	+1		no
2c	M + L	no	59**		+101**	**	no
3b	Aesthetasc	no	66*		+108*		no
4b	Legs Coated (C)	no	99		+14		no
4c	C + L	no	56°		+177**		yes

Group numbers and treatments are the same as in Table I.
Statistical significance: *$P < 0.05$, °$P < 0.02$, **$P < 0.01$ (Mann-Whitney U-test).

all treatment groups, both initial direction choice and subsequent search path length were significantly altered by ablation of the right lateral flagellum or by removal of aesthetasc hairs regardless of the presence (groups 1b, 3b, and 4c) or absence (group 2c) of the medial flagellum. In contrast, glue-coating all walking legs (group 4b) did not change initial direction choice nor search path length (Tables I and II), and ablation of the medial flagellum before (group 2b) or after (group 1c) ablation of the lateral flagellum had no effect on any of the measured behavioral parameters.

SEM showed that the aesthetasc hairs of animals in treatment group 3 were indeed removed. Even in the least effective shaving (Fig. 2), only the bases of some sensilla remained. The significant decrease in the number of correct initial direction choices and the concomitant increase in search path length caused by aesthetasc shaving was not as great as the decrease caused by lateral flagellum removal; the difference is significant in itself (Table II).

In contrast to lobsters in other treatments, only leg-coated lobsters with unilateral ablation of the right lateral flagellum (group 4c) made a significantly higher number of initial direction choices to the left (*i.e.* intact) side ($X_r^2 = 9.33$; $P < 0.01$) regardless of stimulus direction. In many of the trials these lobsters made complete left-turning circles while searching (circus movements, Table II). Besides becoming more erratic these animals searched more slowly, and the increase in length of their search paths was significantly greater ($P < 0.01$) than that of lobsters with only lateral flagellum ablations (Table II). Outside the experimental observation regime, during feeding such lobsters had difficulties locating their daily food.

DISCUSSION

Since none of the experimental manipulations altered alert latency, and assuming that latency across animals and experiments is correlated with detection threshold, we conclude that the lobsters' threshold for odor detection and identification at this stimulus concentration was not affected by unilateral antennule ablations and/or glue-covered legs. The results of experiments 1 and 2 demonstrate the importance of lateral flagellar chemoreceptors for the extraction of directional information from a chemical stimulus field. This is reflected in the dramatic shift in correct initial direction choice from nearly 100% to roughly random following
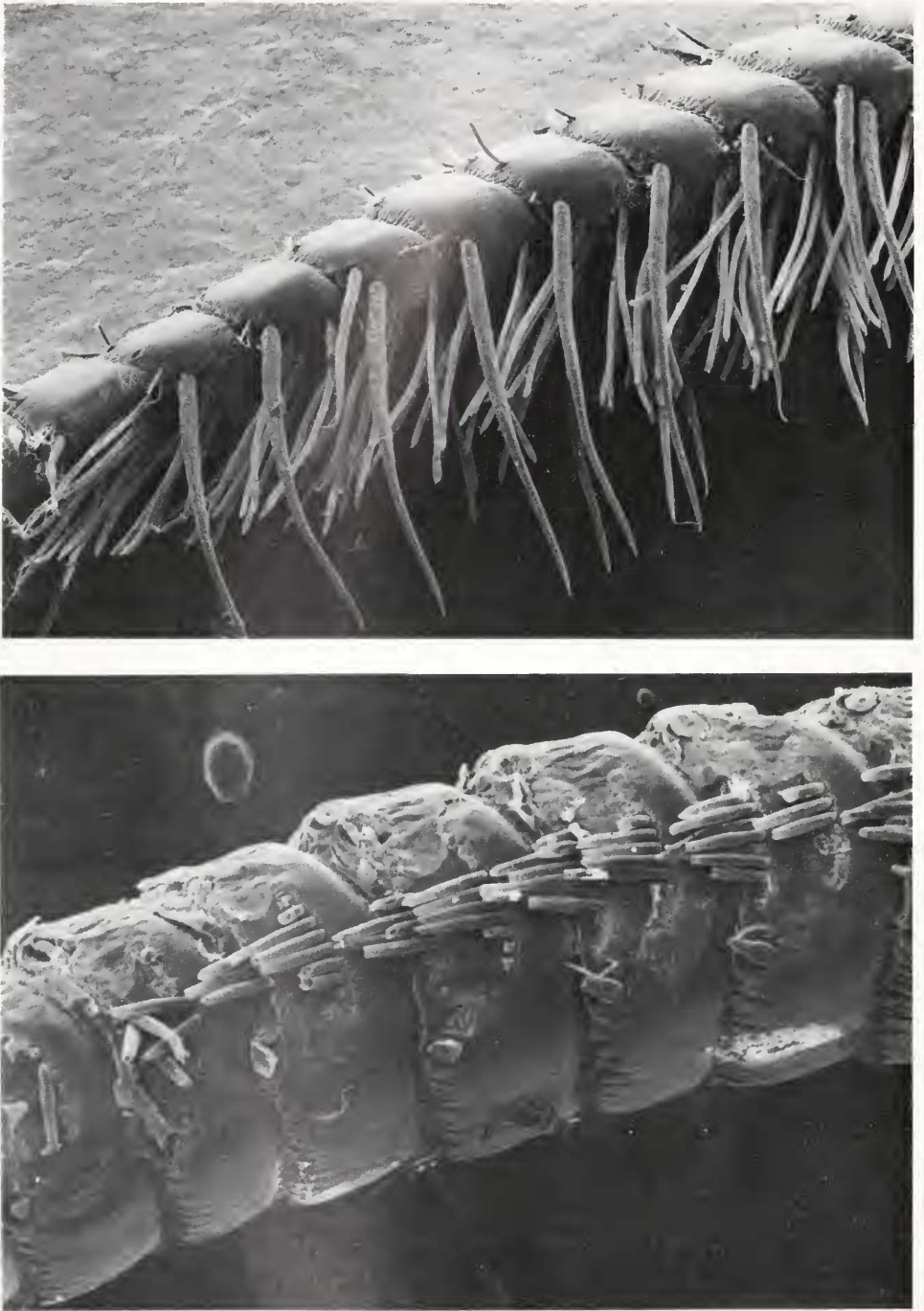
FIGURE 2. SEM of portion of lateral flagellum of antennule. Top: (A) Normal rows of 8–12 aesthetasc hairs, 2 rows per segment, flanked by much larger guard hairs. Bottom: (B) Aesthetasc and guard hairs shaved off at base; in this worst example several remaining aesthetasc stumps contain only proximal segments of receptor dendrites.

unilateral ablation of the lateral flagellum. The same effects are seen when search path length is used as a measurement of orientation efficiency. Ablation of the ipsilateral medial flagellum either prior to or following lateral ablation had no effect on searching behavior, indicating that the input from medial flagellum receptors was not necessary for efficient orientation to odors.

Removal of aesthetasc sensilla alone was sufficient to cause significant changes in orientation ability, but it did not affect initial direction choice as much as entire lateral flagellum ablation (Table II). Therefore, input from other, unidentified lateral flagellum chemoreceptors may aid in orientation. There is both physiological (Fuzessery, 1978) and morphological evidence (Laverack, 1964; Derby, 1982; Gleeson, 1982) for the existence of non-aesthetasc receptors. Since the lateral flagellum is adapted to temporal and spatial sampling of odor space through a combination of its morphology and flicking behavior (Schmitt and Ache, 1979), one could hypothesize that the entire chemosensory input from this flicking appendage is useful for spatial orientation. Yet, the aesthetasc sensilla probably carry the bulk of the information if only by the sheer number of their afferent neurons, about 400 per sensillum (Oleszko-Szuts and Atema, 1977). The behavioral experiments reported here support this notion and extend the results of antennule impairments obtained for spiny lobsters (Reeder and Ache, 1980) by identifying the aesthetasc input as the main but not the exclusive source of directional information. The alternate explanation that the remaining aesthetasc hair bases retain partial function cannot be rejected, but is in our opinion less likely, based on electron microscopic observation of receptor morphology. The base of the aesthetasc hair is made of thick, lamellated cuticle, lined inside with supporting cells. At the level of the transition from the base to the distal portion, inside the hair are the ciliary junctions of the receptor cells (Oleszko-Szuts and Atema, 1977). Thus all of the receptor cell distal segments were removed in the incomplete shavings. Interactions of stimulus and receptor molecule presumably occurs in the ciliary distal segments.

If lobsters are using tropotaxis to make their initial direction choice, unilaterally ablated animals would be expected to show preferential turning toward the intact side regardless of the direction of the stimulus (Fraenkel and Gunn, 1961), resulting in circus movements, *i.e.* turning circles in the direction of the intact side when stimulated. Such circus movements in chemical gradients were described for spiny lobsters with unilateral antennule ablation (Reeder and Ache, 1980) but they were not seen in *Homarus americanus* (McLeese, 1973). In our experiments preferential turning to the intact side and circus movements (Table II) were only seen when laterally ablated lobsters also had the propodus and dactylus of their walking legs coated with glue. Such coated and ablated lobsters also showed greater search path errancy compared to lobsters with only lateral flagellum ablations (Table II). These results demonstrate that leg receptor input does play a secondary role in spatial orientation in a chemical stimulus field; this role becomes apparent when antennular chemoreception is disrupted. However, in otherwise intact lobsters, leg chemoreceptor input was not essential for efficient orientation.

The possibility of chemically stimulated rheotaxis can not be overlooked. Under this hypothesis, a lobster is stimulated by the biologically significant odor of food to search with mechanoreceptors in the ever-present flow gradients. In general, the chemical senses are closely allied with mechanoreceptors, both morphologically and functionally.

In animals such as lobsters, which regularly lose appendages to predators, in social interactions, or through molting disturbance, overlap and redundancy of sensory input must be very important. Our results indicate that when the main

chemosensory input to spatial orientation is lost, other inputs can take over, at least partially. This behavioral recovery of function was not complete in the short duration of these experiments (days), but may well improve over time (weeks) as suggested by studies on hermit crabs (Hazlett, 1971) and lobsters (Atema *et al.*, 1981).

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